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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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THE FERTILE SPECIES HYBRID, PINUS MURRAYBANKSIANA

F. I. Righter and Palmer Stockwell

The species hybrid between the lodgepole pine, *Pinus contorta* var. *latifolia* Englem. (long known as *P. Murrayana* Grev. & Balf.) and the jack pine, *P. Banksiana* Lamb., has proved to be of considerable interest. In the first place, production of this hybrid throws light on the relationship of two economically important North American pines. Secondly, its good form and rapid growth may indicate hybrid vigor, or heterosis.

The history of this hybrid, produced at the Eddy Arboretum, Institute of Forest Genetics, Placerville, California, began in April, 1939, when pollen-bearing strobili of the jack pine were collected from a tree grown in the Eddy Arboretum from seed obtained from Michigan. The pollen was used on June 9 and 12 to pollinate previously bagged ovulate conelets of a lodgepole pine growing at an elevation of 5700 feet in El Dorado County, California, on the west slope of the Sierra Nevada. The breeding techniques used have been described by Cumming and Righter (1948). In May, 1940, both wind-pollinated and hand-pollinated conelets on the El Dorado County lodgepole pine were bagged for protection from insects and squirrels during the period of seed maturation. The following October, 43 wind-pollinated and 34 hand-pollinated cones were harvested from this tree. The wind-pollinated cones yielded a total of 905 seeds with a viability of approximately 30 per cent, and the hand-pollinated cones yielded 700 seeds, approximately 6 per cent of which were viable. Hybrid seeds from the hand-pollinated cones germinated 3 days sooner on the average than seed of equal weight from the open- or wind-pollinated cones, and the hybrid seedlings displayed, from the outset, a faster growth rate than the wind-pollinated seedlings (Righter, 1945). At 3 years of age the average height of the hybrids was 23.8 inches, while the wind-pollinated lodgepole pine averaged 13.3 inches in height. Typical plots of 3-year-old progenies are shown in Figure 1.

At the age of 3 years, 15 hybrid seedlings were paired with 15 wind-pollinated seedlings in a plantation "t" test (Fisher, 1941) consisting of 5 pairs of plots of 3 seedlings each. The average height of the seedlings from the hand pollinations at the age of 7 years was 4.9 feet, while the wind-pollinated seedlings averaged 2.6 feet in height, a highly significant difference.

Some of the hybrid seedlings obtained from the controlled crossing produced strobili of one sex, or of both, when 2 years old (at the beginning of the third growing season). Reproductive activity increased until at 6 years it was possible to place 50 pollination bags, enclosing more than 200 conelets on 12 of the hybrid

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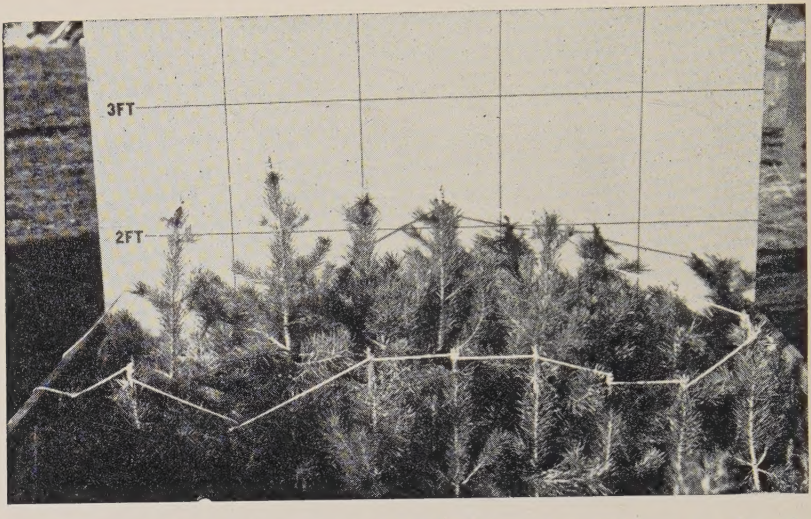

Fig. 1. In the front row with twine tied from top to top are lodgepole pines. In the back row, and similarly marked are the hybrids between lodgepole and jack pine. All are three years old.

seedlings. None of the seedlings from wind pollination produced catkins or conelets until the age of 6 years, when a few strobili of one sex or of both were borne by some of the trees in the plantation test. However, flower production (both sexes) has been reported previously on jack pine at the age of 3 years, and on lodgepole pine at the age of 4 years (Righter, 1939). In another instance ovulate strobili were observed on 2 year old jack pine.

Pollen of the hybrid (fig. 2) was found to be 40 to 50 per cent abortive while that of the parent species is normally only 5 to 10 per cent abortive. Seed-production data, however, indicate that the hybrid is similar to the parents in its output. Thus, an average of 13 sound seeds per cone was obtained from wind-pollinated cones of 2 lodgepole pine trees and an average of 13.1 sound seeds per cone was obtained from wind pollinations and from backcrossing jack pine onto several of the hybrids. This disparity between the production of sound seed and pollen sterility may be explained by two facts. First, from several to many pollen grains usually enter each pollen chamber and are available for fertilizing the egg cell. Second, from 3 to 5 archegonia are normally initiated, but usually only one of these matures and forms a functional egg cell. Thus one viable pollen grain from the several that enter the pollen chamber and one functional egg cell from the 3 to 5 archegonia that are initiated would insure complete fertility (Stockwell, 1939).

The vegetative vigor and reproductive precocity of the hybrid led to an investigation by Buchholz (1945) into the embryological aspects of hybrid vigor in this cross. The same El Dorado lodgepole pine seed tree was used, but the pollen used in making the cross for Professor Buchholz was a mixture obtained from several trees of jack pine growing in the Eddy Arboretum. Buchholz determined that the rate of development of the embryo in the resulting hybrid seeds exceeded that in the natural seeds of the parental species.

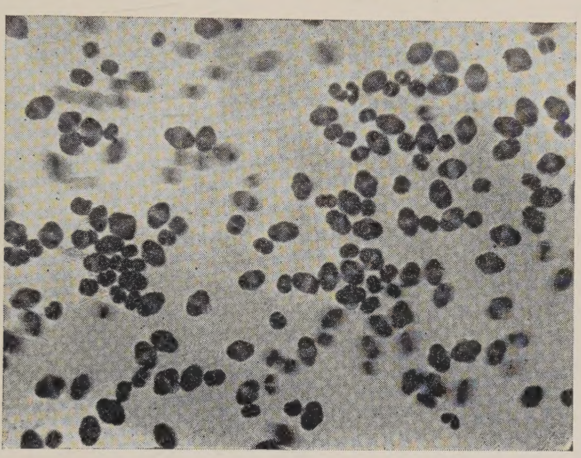

FIG. 2. Pollen of the hybrid between lodgepole pine and jack pine showing approximately 50 per cent abortion.

Additional seeds obtained from the above cross were germinated and the seedlings were compared in nursery tests with the natural progeny of, first, the same lodgepole pine seed-tree and, second, jack pine. Conclusive results with respect to vegetative vigor were not obtained from these tests. Exceptional variation in vigor among individuals in the hybrid plots in both tests indicated that the seed might have been mixed in weighing or that pollination had not been controlled completely. In both tests the hybrids were slightly taller on the average than their competitors, but the differences were not statistically significant.

Both jack pine and the hybrid grow faster than lodgepole pine. Any seed mixture or lack of pollination control, where lodgepole pine was the seed parent, would have resulted in seed of lodgepole pine and the hybrid being mixed and sown together with a consequent reduction in average growth rate. Because of the variability of the hybrids and the fact that their average growth equalled or slightly exceeded that of jack pine it may be assumed that the hybrids at least equal, or probably surpass jack pine in growth rate.

In 1944 the cross was repeated on the same El Dorado County lodgepole pine seed tree with a mixture of pollen from several jack pine trees. Seeds obtained from this cross were tested

TABLE 1. DISTINGUISHING CHARACTERS OF P. CONTORTA VAR. LATIFOLIA, P. BANKSIANA AND × P. MURRAYBANKSIANA.

Distinguishing characters	*P. contorta* var. *latifolia*	*P. Banksiana*	× *P. Murraybanksiana*
Branches	stiff, ascending, straight	flexible, often drooping, sinuate	stiff, ascending, straight
Spring shoots	glaucous	glabrous	± glabrous
Strobili	15–20 mm. long	6–8 mm. long	8–12 mm. long
Open cones	50–70 mm. long; 35–40 mm. diam. recurved	4–5 mm. long; 3–4 mm. diam. incurved	3–4 mm. long; 2.5–3.5 mm. diam. recurved
Cone scales	opening regularly at maturity	opening irregularly and incompletely at maturity	opening regularly and completely at maturity
Apophyses	moderately carinate	usually depressed or plane	usually plane
Prickles	slender, recurved, to 5 mm. long	minute or absent	absent to 1 mm. long

against the natural progeny of the seed parent in a "t" test, consisting of 10 pairs of plots of 10 seeds per plot at a spacing of 12 inches between rows. Germination records were taken every 4 days; there was no statistically significant difference in time of germination between the hybrid and the parental form. At the age of 2 years, the average heights of the hybrids and the natural progeny were 8.9 inches and 6.6 inches, respectively, a highly significant difference.

In 1945, conelets on hybrid seedlings were pollinated with a mixture of jack pine pollen from several trees. Seeds from this backcross were tested in the 1947 nursery against jack pine seeds obtained from the Chippewa National Forest, Minnesota. This test, started on May 7, consisted of 10 pairs of plots, after one pair had been discarded because no seedlings survived in the jack pine plot. There was no difference in time required for germination. Sixty per cent of the hybrid seeds germinated and 27 per cent of the jack pine seeds germinated. At the age of 1 year the average heights of the hybrids and the jack pine seedlings were 3.8 inches and 2.5 inches, respectively, a significant difference. The averages are based on 69 hybrids and 34 jack pine seedlings, or approximately 7 hybrid seedlings and about 4 jack pine seedlings per plot. A number of very weak jack pine seedlings were excluded in computing plot means.

Although the results of these experiments do not constitute conclusive evidence that the backcross is superior to jack pine in height at the age of 1 year, they do indicate that it is distinctly superior on the average to lodgepole pine in vegetative vigor and that it is equal to or possibly superior to jack pine.

Segregation of characters in the progenies of this hybrid will be studied when the seedlings have matured sufficiently to permit analysis.

The two parental species of this hybrid are very similar in all except cone characters. The close relationship indicated by their morphology (table 1) is borne out by the crossing tests. The hybrid is similar vegetatively to the parents; its cone is intermediate.

In order to preserve its identity in the literature as a hybrid and to indicate its derivation, it is proposed that this hybrid be known as × *Pinus Murraybanksiana.* This name was chosen because the lodgepole pine has long been known to western botanists, as *P. Murrayana* and because it would be difficult to coin a satisfactory name from the accepted tri-nomial *P. contorta* var. *latifolia.*

× **Pinus Murraybanksiana** hybr. nov. Arbor hybrida fertilis (*Pinus contorta* var. *latifolia* Engelm. × *P. Banksiana* Lamb.), forma *P. contorta* var. *latifolia* similis; recta, pyramidata-angustata; trunco excurso, ramis verticillatis, adscencis; ramulis multinodis, plerumque glabris, levibus; foliis binis, 4–5 cm. longis, rigidis, obscuro-viridibus; canaliculis resiniferis medianis; hypodermis biformi; vaginis 5–7 mm. longis, pallida-fuscis, membranaceis, erosis, recurvis ultimum, iulis staminiferis 8–12 mm. longis, ochrofuscis; conis sessilibus, inaequalibus, anguste-ovatis, 5–7 cm. longis, fuscis; apophysis planis vel pauciens carinatis, umbonibus planis vel pauciens convexis; spinis brevibus, tenuibus, fragilibus, recurvis; seminibus fertilibus, ca. 3 mm. longis, obscure triangularibus, fuscis; alis angustis, membranaceis, ca. 1.5 cm. longis.

Type. Institute of Forest Genetics, Placerville, California, April 24, 1947, *Stockwell* and *Cumming 2015* (Herbarium University of California, Berkeley, 773157; isotypes distributed). Specimens of parental species: *P. contorta* var. *latifolia, Stockwell* and *Cumming 2013; P. Banksiana, Stockwell* and *Cumming 2014.*

Institute of Forest Genetics, a branch of the California Forest and Range Experiment Station maintained by the Forest Service, USDA, in cooperation with the University of California, Berkeley.

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THE SOLANUM NIGRUM COMPLEX IN PACIFIC NORTH AMERICA

G. Ledyard Stebbins, Jr. and Elton F. Paddock[1]

In the large genus *Solanum,* perhaps the most widespread species-group is that contained in the section Morella, and centering about *Solanum nigrum* L., often known as "deadly nightshade." It consists of weedy perennials or annuals, many of which have become adventive in regions far from their original habitats. In addition, practically every continent and floral region has its indigenous members of the complex. These facts, as well as the great variability of the species, combine to make the group very difficult taxonomically. Many of the more conservative botanists, such as Gray (1886, p. 227) recognize only one species in the entire complex. On the other hand Dunal (1852, pp. 28–387), in his monographic treatment of the genus has recognized no less less than 53 species in this section. An even larger number has been recognized by Bitter (1912, 1913) in his several publications on the genus.

Various members of the complex have from time to time been subjected to cytogenetic analysis. Jorgenson (1928) dealt primarily with the European species, true *S. nigrum* L. and *"S. luteum"* (= *S. villosum* Lam.). He showed that these two species have different chromosome numbers, 2n = 72 and 2n = 48 respectively, and can be hybridized only with the greatest of difficulty. Nakamura (1937) found that the plants growing in Japan and classified as *S. nigrum* actually comprise two distinct species, the typical *S. nigrum* with 72 chromosomes and a diploid with 24 chromosomes, which he named *S. photeinocarpum* Nakamura. Cytological studies by other authors (Tokunaga 1934, Ellison 1936) have confirmed the existence of several different chromosome numbers within the complex.

Our attention was called to this complex by two observations. In the first place, the senior author noticed that the small-flowered straggling perennial which passes as *S. nigrum* in California looked obviously different from the larger flowered, thin-leaved annual which he had previously recognized by that name in the eastern United States. A count of its chromosomes showed that it was a diploid, with 2n = 24 chromosomes. In the second place, the junior author continued an exploration of the complex, only to find that two different chromosome numbers exist among the plants passing as *S. Douglasii* Dunal. Plants from the San Francisco peninsula were hexaploids with 2n = 72 chromosomes, while those from Monterey, the type locality for the species, and from locations throughout central and southern California were found to be diploid, with $2n = 24$.

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[1] Parts of this study were carried out by the junior author during the tenure of a Mary S. Muellhaupt post-doctoral scholarship, granted by the Ohio State University.

These observations led to a cytogenetic study of the complex by the junior author, with special emphasis on the origin of the 72 chromosome form passing as *S. Douglasii.*

This paper aims to present only the taxonomic implications of the cytogenetic investigation the complete results of which will be published elsewhere. From the taxonomic point of view, perhaps the most important fact discovered is that incompatibility as well as weakness and partial sterility of F_1 hybrids are found in crosses between members of the complex having the same chromosome numbers as well as between those with different numbers. This confirms the fact previously established by other cytogeneticists studying the complex, that several distinct species are present in it. On the other hand, hybrids between forms of typical *S. Douglasii* differing in such characters as serration and pubescence of the leaves, as well as size of the flowers, were completely fertile. This indicates that many, if not most, of the species erected by Dunal and Bitter on such trivial characters as these are invalid. Furthermore, the incomplete nature of many of the sterility barriers, as well as the occasional presence of male sterility in wild individuals clearly belonging to a good species and not of hybrid origin, suggests that in this complex some of the diploid entities are species "in the making," which have developed partial but not complete isolating mechanisms separating them from their nearest relatives. This fact undoubtedly contributes considerably to the taxonomic difficulty of the group.

In addition to these cytogenetic observations, the intimate acquaintance which the junior author made with living representatives of this group at all stages of their life history enabled him to observe many diagnostic characters not previously recognized. He showed that the hexaploid passing as *S. Douglasii* could always be distinguished morphologically from the typical diploid species, even before its chromosome number was known. This hexaploid, originally believed to be an endemic of the San Francisco Bay region, was later found to be identical with the common large-flowered *Solanum* of Chile, for which the oldest valid name is *S. furcatum* Dunal. It is an introduced weed in the San Francisco area, as well as at Westport and Trinidad, California, and in a few places on the Oregon coast. Furthermore, the authors have found that the American diploids can be distinguished morphologically from the typical European *S. nigrum,* and so are considered specifically distinct from it. Finally, it was found that the form passing in California as *S. nigrum* var. *villosum* is not the European *S. villosum* Lam., but a very different species, *S. sarachoides* Sendt., native to South America.

Therefore, while the authors are far from possessing enough knowledge to enable them to revise this difficult complex as a whole, they feel justified in placing on record their observations on the identity and relationships of the representatives of the group which they have studied. A few synonyms have been given with the descriptions of some of the species in order to indicate the opinion of the authors as to the correct disposition of these names. However, no attempt has been made to give a complete synonymy of any of them. They may be identified by the following key:

A. Plants conspicuously and persistently villous or hirsute; ripe berries greenish, yellow, or reddish; seeds 1.8–2.2 mm. long.

B. Flowers 3–8 in an inflorescence; apex of pedicel and calyx strongly expanded at maturity, the latter enveloping the lower part of the berry; ripe berry greenish ..... 1. *S. sarachoides* Sendt.

BB. Flowers 1–5 in an inflorescence; pedicel and calyx not or only slightly expanded at maturity; ripe berry yellow or reddish .... 2. *S. villosum* Lam.

AA. Mature growth of plants sparsely pubescent or glabrous; ripe berries black; seeds 1.2–1.8 mm. long, except in the sparingly introduced *S. nigrum* L.

C. Larger inflorescences usually bifurcate, the peduncle deflexed at maturity; flowers relatively large (corolla lobes 6–11 mm. long); filaments unequal in length; mature berries immediately deciduous when ripe, containing 7–34 seeds; straggling perennial .... 3. *S. furcatum* Dunal

CC. Inflorescences rarely bifurcate, the peduncle remaining erect at maturity; flowers large or small; filaments nearly or quite equal in length; mature berries persisting on the plant in the ripe condition (except in *S. americanum*), containing 25–80 seeds; perennial or annual.

D. Flowers large; corolla lobes 6–11 mm. long measured from the base of the corolla; anthers 2.6–4.0 mm. long; style exserted about 2 mm. beyond the anthers; stigma very slightly expanded; bushy perennial .... 4. *S. Douglasii* Dunal

DD. Flowers smaller; corolla lobes 3–7 mm. long; anthers 1.2–2.6 mm. long; style barely exserted beyond the anthers, the stigma enlarged and capitate.

E. Annual or perennial, the leaves firm in texture; inflorescence umbelliform or nearly so; calyx lobes all distinct from each other, reflexed at maturity; surface of berry glossy; stone cell concretions absent or few, rarely more than 3 .... 5. *S. nodiflorum* Jacq.

EE. Strictly annual, the leaves thin in texture; calyx lobes unequal in length, some of them partly fused, not reflexed at maturity

F. Inflorescence mostly umbelliform; anthers 1.4–2.0 mm. long; surface of berry glossy; seeds 1.2–1.8 mm. long; stone cell concretions always present, usually 4 to 8 per berry; berries immediately deciduous when ripe .... 6. *S. americanum* Mill.

FF. Inflorescence always subracemose; anthers 1.8–2.6 mm. long; surface of berry dull; seeds 1.7–2.2 mm. long; stone cell concretions absent, or very small and not more than 1–2 per berry. .... 7. *S. nigrum* L.

The following notes on these seven species are based upon observations of living plants studied both in the wild and in greenhouse cultures at Berkeley, and of the large series of specimens in the Herbarium of the University of California (cited as UC), the Gray Herbarium, Harvard University (GH), the Dudley Herbarium, Stanford University (DS), and the Willamette University Herbarium, Salem, Oregon (Will.). The authors are most grateful to the curators of these herbaria for the loan of these specimens.

1. Solanum sarachoides Sendt. ex Mart. Fl. Bras. 10: 18. 1846. *S. gracile,* sensu Gray, Syn. Fl. N. Am. 2 (1): 228. 1878, and Small, Man. Southeastern Flora 1114, 1933, not Link.

This species, described from Brazil and native to subtropical and temperate South America, has become widely distributed in the United States. In the flowering condition it is not unlike other members of the complex, but in fruit it is entirely different from any other species found in North America. As the berry ripens its pedicel becomes much swollen near the apex and the calyx enlarges to several times its size at anthesis. The greenish berry contains large seeds, like those of *S. villosum* and *S. nigrum,* but these are fewer in number. *S. sarachoides* is diploid, 2n = 24.

The confusion of this species with the very different *S. villosum* Mill. of Europe seems to be based only on the fact that both species have hairy stems and leaves. Their pubescence, however, is very different in character. The stem and leaves of *S. sarachoides* are green and are thinly hirsute, with spreading, slender trichomes, while the pubescence of *S. villosum* is usually denser and more or less appressed, so that the plant looks grayish to the naked eye. The floral and fruiting characteristics mentioned above and in the key are even more distinctive.

The specimens referred to this species have been carefully compared with the description and illustration of Sendtner (*loc. cit.*), as well as with the photograph of the type specimen (Villa das Minos, Uruguay, *Sellow 281*) preserved in the Gray Herbarium. This type was at Berlin. There is no doubt that the specimens from North America agree exactly with it, as well as with other specimens from South America. *Solanum sarachoides* is a rather common weed in arable land throughout the Pacific states, and apparently was introduced at an early date. There are two specimens in the Gray Herbarium that were collected in 1877, one from between Virginia City and Carson City, Nevada (*Hooker & Gray s.n.*), and one from Multnomah County, Oregon (*Howell 333*). It has been usually identified as *S. nigrum* L. var. *villosum* Mill., or as *S. villosum*. The following specimens may be considered typical.

British Columbia. Vancouver Island, *Macoun 698* (GH); Fraser River, *Condit* in 1909 (UC).

Washington. Klickitat County: near Bingen, *Suksdorf 1480* (GH, UC). Jefferson County: near Port Townsend, *Barber 158* (GH), *Otis 2343* (UC, DS).

Oregon. Portland, *Nelson 1729* (GH); Minto's Island, Salem, *Nelson 2927* (GH). Umatilla County: Milton, *Brown 39* (UC). Union County: Fry's Point, alt. 1000 m., *Sheldon 9036* (GH).

California. Solano County: Vallejo, *E. L. Greene, s.n.* (GH). Mono County: Mono Lake, *Congdon* in 1894 (GH). Humboldt County: Eureka, *Tracy 3074* (UC). San Mateo County: near Moss Beach, *Wiggins 8164* (UC, DS). Los Angeles County: La Verne, *Wheeler 1130* (UC). Orange County: Santa Ana River, *Booth 1344* (UC). Amador County: Ione, *Braunton 1200* (UC).

2. **Solanum villosum** Mill. Gard. Dict. ed. 8, no. 2. 1768; Lam. Illustr. 2: 18. 1793. *S. luteum* Mill. (*op. cit.*), no. 3, 1768. *S. alatum* Moench. Meth.: 474, 1794; Small, Man. Southeastern Flora 1114, 1933.

This European species is a rather uncommon introduction in the United States. It is characterized by its usually dense, grayish-villous pubescence; rather small, ovate leaves; yellowish or reddish berries; and large seeds. It is a tetraploid, 2n = 48. The only specimen seen from western North America is from a plant cultivated in the University of California Botanical Garden, Berkeley (*McKay* in 1930, UC). A collection from Pensacola, Florida (*Curtiss 6493* GH, UC) consists of typical material from the eastern United States.

3. **Solanum furcatum** Dunal, Solan. Gen. aff. Syn. 13, n. 52. 1816. *S. chenopodioides* Lam. Illustr. 2: 18. 1793, in part. *S. rancaguense* Dunal, ex DC. Prodr. 13: 150. 1852.

Perennial, mostly straggling or reclining on other plants; the stems long and slender, with internodes longer in proportion to stem diameter than in the other species found in North America; peduncles slender, becoming strongly deflexed as the berries ripen; inflorescence racemose to cymose, the common peduncle often bifurcate at the apex; flowers large, the corolla lobes 6–11 mm. long, the sinuses shallow; filaments 1.0–2.3 mm. long, unequal; style projecting well beyond the anthers, stigma dark, capitate; berries small, deciduous immediately after ripening, mostly with 12–25 seeds and many large stone cell concretions. Chromosome number, 2n = 72.

The fine series of specimens of this species from Chile in the Gray Herbarium all agree in the characteristics given above, although they vary considerably in leaf shape, flower size, etc. They represent collections from all parts of central Chile, and include a duplicate of the type collection (Chili, *Dombey,* as *Witheringtonia rubra*). The following specimens from North America have been seen.

OREGON. Ballast, Linnton, *Nelson 505* (GH, DS). Curry County: The Heads, Port Orford, *Peck 20389* (Will.); near Harbor, *Peck 21262* (Will.); Port Orford, *Keck and Clausen 3428* (DS); Gold Beach, *Hoyt 44* (DS). CALIFORNIA. Humboldt County: Trinidad, *Tracy 16749* (UC). Mendocino County: Noyo, *Duncan 215* (DS); Westport, *Paddock 167, 168* (UC). San Mateo County: San Pedro Point, *Brandegee* in 1908 (UC); Mussel Rock, *Paddock 19* (UC).

Solanum furcatum looks superficially like *S. Douglasii* Dunal, but is easily recognizable upon close examination by the characters given in the above key. *S. furcatum* is apparently the commonest species of this complex in Chile. It is apparently the Chilean plant referred to by Lamarck (loc. cit.) in his description of *S. chenopodioides,* and has been given this name by some students of the Chilean flora. Lamarck, however, had two different plants in mind when he described this species. After the original description he cites as a locality first "Ex ins. Mauritiana," then "An *S. chenopodioides* Feuillee obs. 2. t. 14." From this it seems evident that Lamarck was describing primarily the plant from Mauritius. This is even clearer from the amplified description in his Encyclopédie Méthodique (1797, p. 290), in which he characterizes the plant as having 3 or 4 small flowers in an inflorescence. The species which best fits this description is the pantropical weed, *S. nodiflorum* Jacq. The type locality for *S. nodiflorum* is Mauritius, and it is the only species of the section which grows both on that island and in Chile.

In genetic behavior as well as chromosome number, *S. Douglasii* and *S. furcatum* are very different. The junior author was unable to obtain hybrids between them, even though attempts were made in both directions. Seedless, parthenocarpic fruits developed when *S. furcatum* was used as the ovulate parent. However, an artificially produced autotetraploid *S. Douglasii* produced pentaploid hybrids when crossed with the hexaploid *S. furcatum.* These hybrids were vigorous and partly fertile, setting 5 to 8 seeds per berry after artificial selfing.

In North America, *S. furcatum* is certainly a recent introduction. It occurs abundantly in only three restricted localities, all near seaports, namely San Francisco and Westport-Noyo in California, and Port Orford, Oregon. In the Westport-Noyo region the junior author has collected a distinctive narrow-petaled strain

(*Paddock 168,* UC), and one having entire-margined leaves (*Paddock 167,* UC). One or both of the writers have observed *S. furcatum* at all of its known stations in North America except for Linnton, Oregon, and at all it looks and behaves like a recently introduced weed.

4. Solanum Douglasii Dunal, ex DC. Prodr. 13: 48. 1852. *S. nigrum* var. *Douglasii* Gray, Bot. Calif. 1:538. 1876.

From coastal north-central California south to Baja California, eastward through Arizona, New Mexico, and northern Mexico, southeastward at higher altitudes throughout Mexico and probably Central America. This is the common native member of the section throughout the southwestern United States and Northern Mexico, and has been well described in the various floras. Its bushy, perennial habit, large leaves and flowers, and numerous, persistent, many-seeded black berries serve to distinguish it easily from any other species found in this area. It is a diploid (2n = 24).

In California, where *S. Douglasii* is native and *S. nodiflorum* an introduction, the two species are quite distinct from each other. Intermediate forms have been found only in one locality, at Hecker Pass northeast of Watsonville, Santa Cruz County. In Central Mexico, however, both species are native, and they are much less well defined. All specimens seen from the tropical parts of Mexico are typical *S. nodiflorum,* while those from the higher plateau, as about Mexico City, seem indistinguishable from the northern *S. Douglasii.* In certain intermediate areas, however, as at San Luis Potosí, several specimens intermediate in character have been collected. Some of these have partly or completely abortive and sterile pollen. A few, however, have normal pollen and occasional plants with abortive pollen occur among those typical both of *S. Douglasii* and *S. nodiflorum.*

This confusing situation is perhaps explained by the hybridization experiments of the junior author. He has found that *S. Douglasii* and *S. nodiflorum* can be reciprocally hybridized rather easily, but that the F_1 hybrids have from 50 to 100 per cent of abortive pollen, and consequently are only partly fertile. Nevertheless, they yield vigorous, partly fertile progeny when back crossed to either parent. On the basis of this evidence one would not expect extensive intergradation between the species unless they had been growing side by side for some time. Nevertheless, once F_1 hybrids and their derivatives became established, they would, because of their vigorous growth and perennial habit, yield a large number of back cross progeny, which would tend to obscure the initial distinctness between the species. *Solanum Douglasii* and *S. nodiflorum* may therefore be looked upon as "borderline species," which are separated by both ecological and genetic isolating mechanisms, neither of which is perfectly developed.

The northernmost station known for *S. Douglasii* is Rockport, Mendocino County, California (*Paddock 165,* UC). It is not known between here and southwestern San Mateo County, where it is rather common. From thence southeastward it is so well known and easily recognized that citation of specimens seems unnecessary.

5. **Solanum nodiflorum** Jacq. Ic. Pl. Rar. 2: 288. 1786. *S. chenopodioides* Lam. Illustr. 2: 18. 1793, *pro parte. S. photeinocarpum* Nakamura et Odashima, Jour. Soc. Trop. Agr. 8: 54, fig. 2. 1936; Cytologia, Fujii Jubil. Vol.: 58. 1937. *S. nigrum* vars. *Dillenii* and *nodiflorum* Gray, Syn. Fl. North America 2 (1): 288. 1878. *S. nigrum,* sensu Jepson, Man. Fl. Plants Calif. 892. 1925, not L.

Straggling perennial; stems rounded or angled; leaves entire or sinuate-dentate; inflorescences umbelliform; calyx lobes small, thick and reflexed at maturity; flowers small; filaments and anthers variable in length, the latter 1.5–2.4 mm. long; berry shiny black, many-seeded, usually without stone cell concretions, or with 1 to 4 small ones. Chromosome number, $2n = 24$.

This and *S. nigrum,* are the two commonest, most widespread and most variable species of the section Morella. It apparently is an ubiquitous weed in the tropics of both hemispheres, although probably native only to the New World. The type locality is the island of Mauritius. In the western United States it is clearly introduced, probably from Mexico. It is common throughout coastal California, having been described in all of the floras as *S. nigrum.* It extends northward into Washington. Its occurence in southern Japan and Formosa has been discussed by Nakamura (loc. cit.) who described it as a new species, *S. photeinocarpum.* From seeds kindly sent by Dr. Nakamura, we have grown plants which are morphologically very similar to those collected in Berkeley. Hybrids between these two forms had better than 50 per cent fertility of pollen and seed.

The typical form of *S. nodiflorum,* with entire leaves, rounded stems, narrow corolla lobes, and short filaments, is the most common one in the tropics. In sub-tropical or warm-temperate regions the more common type has dentate leaves, angled stems and longer filaments. In a weed of this type, however, geographical subspecies or varieties are very poorly defined. In California the dentate leaved form is definitely the more common, but many specimens morphologically indistinguishable from the tropical form have been collected in southern California, where they do not show any difference in habitat preference from the dentate-leaved plants, and where all sorts of intergradations and recombinations of the character differences noted above can be found. After thorough acquaintance in the field with this species in many different countries, one might be justified in recognizing geographic segregates, but at present the wisest course is to recognize that we are concerned with an extremely variable species.

Citation of specimens of this common weed seems unnecessary; nearly all of the specimens from California identified as *S. nigrum* belong to it. In Oregon and Washington there occur puzzling integrades between it and *S. americanum,* but field studies would be necessary to determine the true status of the plants occuring in this region.

6. Solanum americanum Mill. Gard. Dict. ed. 8, no. 5. 1768. *S. pterocaulon* Dunal, Hist. Solan.: 153. 1813. *S. Besseri* Weinm. ex Roem. et Schultes, Syst. 4: 593. 1819. *S. nigrum* sensu Gray, Syn. Fl. N. Am. 2 (1): 227. 1886, and other American authors, in large part, not L.

Similar to *S. nodiflorum,* but always annual; leaves usually larger and thinner in texture; inflorescence usually umbellate but occasionally subracemose; flowers somewhat larger than those of *S. nodiflorum,* the corolla lobes 4.5–7.0 mm. long, from the base of the corolla; calyx thin, green, its lobes short-deltoid, unequal, some of them partly united, not reflexed at maturity; anthers 1.3–2.0 mm. long, the filaments about half as long; berries black, lustrous, many-seeded, with 2–8 stone cell concretions of moderate size. Chromosome number, $2n = 24$.

Throughout the eastern United States, south to northern Florida and Texas, west to the Great Plains, and perhaps Oregon and Washington.

With his original description, Miller does not cite the locality from which his specimens came, nor does he cite any specimens. However, the Latin description is followed by the following remark: "American nightshade like the common sort, with a small purplish flower, and smaller black berries." The flowers of the eastern American plant may be either purplish or white, but the berry is usually smaller than that of European *S. nigrum.* Since Miller characterized his species as "like the common sort," one can infer that he was describing the small herbaceous annual of temperate eastern North America, which resembles the European species considerably more closely than does the larger, sub-perennial plant of the American tropics. It is on this basis that the present authors use the name *S. americanum* for the form of the eastern United States, and *S. nodiflorum* for the tropical weed which has passed as *S. americanum* or *S. nigrum* var. *americanum* in some American floras.

Although some of the specimens from Oregon and Washington identified as *S. nigrum* approach *S. americanum* in some characteristics, others are clearly *S. nodiflorum.* No material seen from west of the Rocky Mountains is unquestionably *S. americanum.*

Typical *S. americanum* from the eastern United States, as represented by both herbarium specimens and greenhouse cultures, is very different from Pacific Coast material of either *S. nodiflorum* or *S. Douglasii.* Furthermore, hybrids between it and these species are partly or wholly sterile. The *S. nodiflorum* × *Douglasii* hybrid has already been discussed under the description of *S. Douglasii.* That between *S. americanum* and *S. nodiflorum* has been produced twice. The first series of hybrids, between a strain of *S. nodiflorum* from Berkeley and one of *S. americanum* from Madison, Wisconsin, were weak dwarfs, which were very hard to keep alive, and flowered abortively when only a few inches tall. They were completely sterile. A second hybridization, between the Berkeley *S. nodiflorum* and *S. americanum* from Ohio, produced vigorous F_1 plants which had about 30 per cent of normal appearing pollen and from 15 to 20 per cent of normal seed set on open pollination. These two species, therefore, are separated by barriers of both hybrid inviability and hybrid sterility, but the barriers in each case are only weakly developed.

One hybridization was made between *S. Douglasii* and *S. americanum,* the parents of the hybrid being from Monterey County, California, and near Columbus, Ohio, respectively. These F_1 plants were vigorous and intermediate morphologically, except that their seeds were smaller than those of either parent. They had about 10 per cent of normal appearing pollen, and set 20 to 25 per cent of the normal number of seeds when artificially selfed. The genetic barriers between the three species *S. americanum, S. nodiflorum,* and *S. Douglasii* all seem therefore to be of about the same degree of development. The genetic evidence, while favoring the status of these entities as "borderline" species, would not prevent their treatment as subspecies of a single species.

The fourth member of this group in the United States, which has not been studied in the living condition but which has the pollen size of a diploid, is *S. interius* Rydb. This form, which was first described from the plains of Nebraska, is in most characteristics intermediate between *S. americanum* and *S. Douglasii.* Furthermore, a study of herbarium specimens suggests that in Nebraska, Kansas, and Texas, *S. interius* grades into *S. americanum,* while in New Mexico there are many intermediates between it and *S. Douglasii.* On the other hand, the seeds of *S. interius* are characteristically larger than those of either *S. americanum* or *S. Douglasii,* while those of the artificial hybrid between the two latter species produced by the junior author are smaller than the seeds of either of its parents. The status of *S. interius* cannot be decided until typical material of it is grown with that of *S. americanum* and *S. Douglasii,* and the necessary hybridizations are made. It is apparently the predominant form of the *S. nigrum* complex in the western Great Plains area.

7. SOLANUM NIGRUM L. Sp. Pl. 186. 1753. *S. Dillenii* Schultes, Oestr. Fl., ed. 2, 1: 393. 1794; non *S. nigrum* var. *Dillenii* Gray, Syn. Fl. N. Am. 2 (1): 228. 1884.

Annual; stems relatively low; leaves variable in shape, but usually entire or only slightly serrate; inflorescence subracemose;

flowers medium-sized, corolla lobes 5.5–7.5 mm. long; anthers 2.1–2.6 mm. long; berries rather large, with a dull surface, many-seeded, the seeds 1.9–2.3 mm. in diameter; concretions absent. Chromosome number, $2n = 72$.

Common and widespread in Eurasia and Africa; sparingly introduced in North America, mostly along the Atlantic seaboard. The plants of this species found occasionally in the central and western states are mostly the strain released by Burbank as the "wonderberry." This has rather large fruits, but is otherwise typical of *S. nigrum.* Its berries, like those of all of our members of this section, are edible and harmless. We find them to have a rather insipid flavor.

The distinctions between true *S. nigrum* and *S. nodiflorum* have been clearly pointed out by Nakamura (1937). *S. americanum* is more easily confused with the European species, since it is also an annual, has corollas of nearly the same size, and sometimes has subracemose inflorescences. The smaller stamens, and smaller seeds are the best diagnostic characters to separate *S. americanum* from *S. nigrum.* Furthermore, the berries of *S. nigrum* completely lack the concretions of stone cells which are found to a greater or lesser degree in all plants of *S. americanum.*

Cytologically, *S. nigrum* is very different from most of the other species of the section, since it is a hexaploid with $2n = 72$ chromosomes. The junior author has found, as expected, that the extremely vigorous hybrid between *S. nigrum* and the diploid *S. americanum* has a very irregular meiosis and 86 per cent of abortive pollen. The difference in chromosome number between these two species gives rise to an additional diagnostic character by which they may be distinguished, namely a difference in the size of the pollen grains. When mounted in water and heated so that they become spherical in shape, pollen grains from herbarium specimens of *S. nigrum* measure $24–27\mu$ in diameter, while those of *S. americanum, S. nodiflorum,* and *S. Douglasii* are only $16–20\mu$ in diameter. The pollen of the hexaploid *S. furcatum* is as large as that of *S. nigrum,* but these two species always can be distinguished from each other with ease. Their hybrid, *S. nigrum × furcatum,* has been found by the junior author to be highly sterile and to have irregular meiotic divisions, in spite of the identity of the chromosome number of the two parents. This hybrid exhibits the growth habit of *S. furcatum.* The only specimen of true *S. nigrum* seen from Pacific North America is the following: near Forestry Building, Portland, Oregon, August 31, 1927, *J. W. Thompson 3663* (DS).

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TWO PROBLEMS IN SALIX DISTRIBUTION

Carleton R. Ball

Two peculiar problems in the distribution of certain North American species of *Salix* have confronted the writer for several years. The first problem is presented by two unrelated species having an extremely extended, but fairly continuous, distribution from south to north. The second problem is concerned with two unrelated species which have a fairly extensive, but finally discontinuous, distribution from east to west. By "unrelated" is meant that the two members of each pair belong to quite widely separated sections of the genus *Salix*.

The geographical direction of distribution given above is from the region of greater abundance to that of increasing scarcity and final disappearance. It is hoped that some one may throw light on the physiological and/or ecological factors governing these peculiar plant distributions.

A. Extremely Extensive South-North Ranges

The two species of *Salix* with greatly extended south-north distribution are *S. lasiandra* (accompanied by its hairy-twigged variety *lancifolia*) and *S. interior* (with its narrow-leafed variety *pedicellata*). Both species range from the latitude of northern Mexico (30°–32° N.) to the Arctic Circle or beyond (67° N.), or some 2500 miles or more. In each case, the species and its variety occur together throughout almost the entire distance.

1. *Salix lasiandra* Bentham, the Pacific or western shining

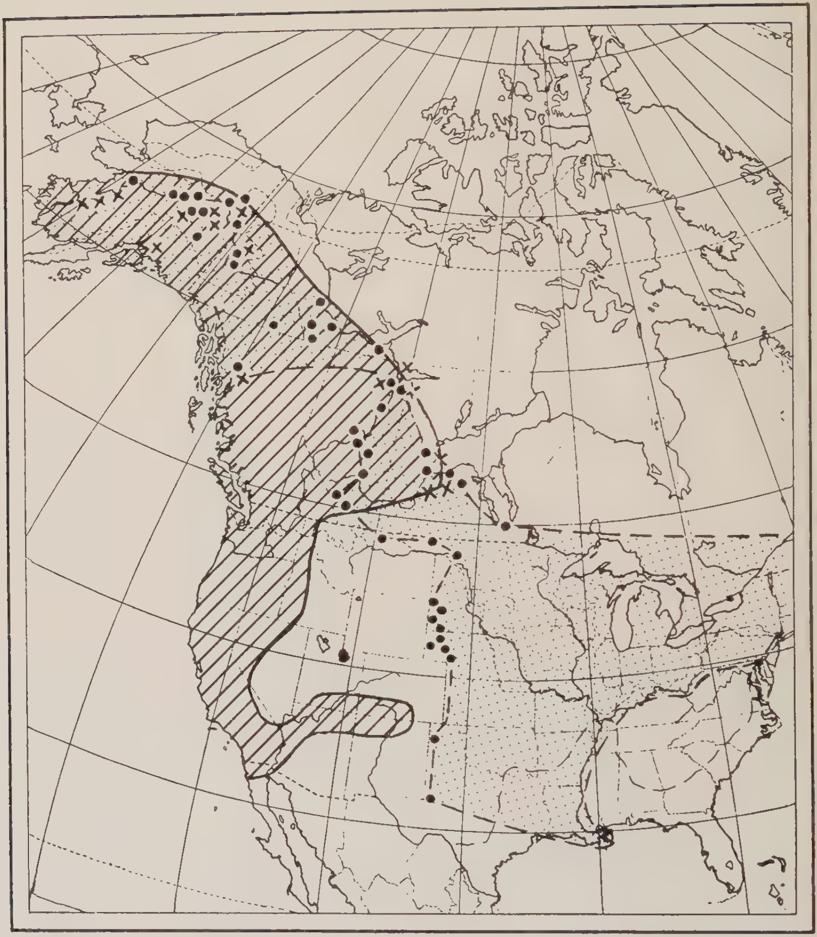

Fig. 1. Distribution of *Salix lasiandra* and its var. *lancifolia* (hatching) and *S. interior* and its var. *pedicellata* (fine dotting). Localities of marginal collections indicated by letter "x" and large dots, respectively.

willow, and its hairy-twigged variety *lancifolia* (Andersson) Bebb, occur from northwestern Mexico to Alaska and Yukon. From the hot climate of Baja California and southern California, they pass northward abundantly throughout California, Oregon, Washington, western Nevada, and Idaho. In the south, a long finger of sparse distribution projects eastward across the northern portions of Arizona and New Mexico and the adjoining southern parts of Utah and Colorado (fig. 1).

In Canada, the species and variety extend northward, with decreasing abundance, across British Columbia and mountainous western Alberta and eastward into the prairies as far as east-central Saskatchewan and thence north at least to the west end of Lake Athabaska in northern Alberta. Farther north and west, the species occurs on the lower Stikine River in northwestern British Columbia near the International Boundary north of Wrangell, and again on the headwaters of the Chilkat River at the northern tip of the Alaskan "Panhandle".

Species and variety occur together at several points on the Yukon and Klondike rivers in the Dawson area of Yukon (64° N.). In Alaska proper, the variety occurs alone at Matanuska, at the head of Cook Inlet in south-central Alaska. It has been found also along the Yukon River at Fort Yukon (Arctic Circle), Blackburn, and even Holy Cross (62° N., 160° W.), as well as on the tributary Tanana River at Salcha Slough, Fairbanks, and Nenana.

The distribution from northwestern British Columbia across Alaska and western Yukon is sparse but fairly continuous. Similar continuous distribution from Lake Athabaska northwestward across the wide expanse of the Peace River and Liard River drainage is in doubt, but collecting has not been sufficient to prove its absence.

The total recorded range covers about 35 degrees of latitude (32° N. to almost 67° N.). It extends across the Lower and Upper Sonoran, Transition, Canadian, and Hudsonian Life Zones, and almost touches the Arctic Zone at various points on the Yukon River from Dawson to Holy Cross.

2. *Salix interior* Rowlee, and its slender-leafed variety (*pedicellata* (Andersson) Ball, range northward from the mouth of the Mississippi River (30° N.) across the United States and Canada to slightly beyond the Arctic Circle in Alaska. Westward of the Mississippi, they (and especially the variety), fan out across the Great Plains almost to the foothills of the Rocky Mountains in the United States and Canada. Eastward, the species ranges up the Ohio Valley, across the mountains, down the Potomac Valley to the District of Columbia, and thence northeastward to Delaware, New Hampshire, New Brunswick, and Quebec. Then the line runs west to southern Manitoba and northwestward to Lake Athabaska, the species and variety occurring together in the Prairie Provinces (fig. 1).

In the Mackenzie River (Arctic) drainage basin of southern Mackenzie, the species (and occasionally the variety) occur on the Slave River (Fort Smith), on Great Slave Lake (Hay River), and on the Mackenzie River (Fort Simpson, Fort Wrigley, 63° N., 123° W.). Westward, on tributaries of the Mackenzie, the species has been found at the mouth of the Nahanni River (61° N., 124° W.), at Fort Liard on the Liard River (60° N., 124° W.), and on the Upper Liard River at 60° N. This is at about 128° W. and near the British Columbia—Yukon Boundary.

In Pacific drainage, the species and variety occur in British Columbia, Yukon, and Alaska. In northwestern British Columbia, the species has been found once on the Stikine River, near the Alaskan border north of Wrangell. In Yukon, species and variety occur at several points on the Yukon and Klondike rivers within some 20 miles of Dawson (64° N., 140° W.). In Alaska, species and variety follow the Yukon River westward, occurring at Circle (66° N., 144° W.), on Porcupine River 40 miles above the mouth (67° N., 144° W.), Fort Yukon (66° 30′ N., 145° W.), between Rampart and Tanana, between Fort Gibbon and Tanana (65° N., 152° W.), and at Nulato (158° W.). On the tributary Tanana River, the species occurs at Fairbanks and Hot Springs and the variety at Nenana. Outside the Yukon drainage, the species has been found at but one point in Alaska, namely, Paxson's (Roadhouse), just south of the divide separating the north-flowing Tanana and the south-flowing Gulkana-Copper River drainages.

The range recorded above covers 37 degrees of latitude (30°–67° N.) or some 2600 miles, and 90 degrees of longitude (68° W. in New Brunswick to 158° W. in Alaska). The Life Zones covered are the Carolinian, Alleghanian, Canadian, and Hudsonian, with the Arctic Zone almost reached at points on the Yukon River.

One striking fact regarding both *S. lasiandra* and *S. interior* is that there is little or no more observable variation in characters between plants collected at the two extremes of this range than between plants collected at any one point within the range.

In these vast ranges, wide differences occur in temperature, precipitation, humidity, length of season, and length of day. Yet these two species seem to show complete ability to adapt themselves to these differences without observable change in characters.

B. Extensive, but Discontinuous, East-West Ranges

Different species of *Salix* which occur commonly in our northeastern and north-central States and adjacent Canada penetrate westward to very different distances. Some, like *S. interior* Rowlee, *S. rigida* Muhl. (*S. cordata* Muhl.), and *S. discolor* Muhl., are replaced in the Rocky Mountains and westward by related species. Others, like *S. amygdaloides* Anders., reach but do not pass the Sierra-Cascade barrier. Still others, like *S. Bebbiana* Sargent, *S. candida* Fluegge, and *S. pedicellaris* var. *hypoglauca* Fern., extend practically to the Pacific Ocean. Two species which penetrate only to the front range of the Rocky Mountains, and that only by discontinuous distribution, are discussed below.

1. *Salix serissima* (Bailey) Fernald, related to *S. lucida* Muhl. of the East and to *S. caudata* (Nuttall) Heller and *S. lasiandra*

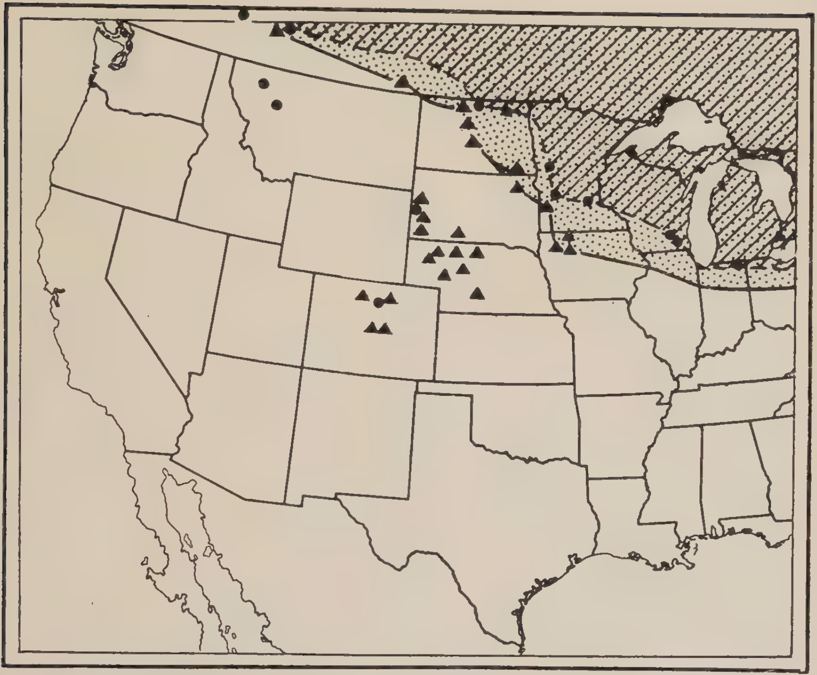

FIG. 2. Southwestern portion of the distribution of *Salix serissima* (hatching and large dots) and of *S. petiolaris* (fine dotting and triangles) in North America, showing relation of the continuous northeastern distribution of these two species to their marginal and discontinuous distributions.

Bentham of the West, occurs commonly from New England and Lower Canada westward. The southern boundary of its range lies along the southern edge of the Great Lakes area to St. Paul and Kandiyohi County, Minnesota, thence northward through Ottertail and Clearwater counties, and westward in North Dakota, in the northern tier of counties (Pembina, Rolette). From here the line runs northwestward to Calgary and the Banff area in southern Alberta. Northward the range extends to Lake Athabaska and southern Mackenzie (fig. 2).

By discontinuous distribution, the species occurs in three separate areas to the south and west of its continuous distribution. The first area includes Flathead (Glacier Park) and Chouteau counties in northwestern Montana, some 150 and 230 miles, respectively, south of Calgary. Far to the west and south of the main distribution are two mountain outposts in South Dakota and Colorado, respectively. In the Black Hills of South Dakota, Professor A. C. McIntosh found it in sedge moor at two localities near Deerfield, Pennington County, in 1928 and 1929. In the Front Range of the Rocky Mountains, Professor Ernest C. Smith collected it at Longs Peak Inn, elevation 9000 feet, on Longs Peak, Larimer County, Colorado, in 1935, 1936, and again in 1943.

The writer previously had presented the known distribution of this species in the United States and Canada in two different papers (Bot. Gaz. 72: 220–22. 1921; Canadian Field Nat. 40: 147–48. 1923). The first paper brought forth a statement from Francis Welles Hunnewell (Rhodora 25: 67–68. 1923) that he had collected *S. serissima* on Longs Peak in 1913 and that the determination had been verified by Dr. Fernald. In the second paper, and again in Deam's Shrubs of Indiana, the writer erroneously credited this collection to Pikes Peak instead of Longs Peak.

The Black Hills locality is about 450 miles from the nearest North Dakota station, and about 500 and 600 miles, respectively, from the two Montana stations far to the northwest. The Longs Peak station is 600 miles from Rolette County, North Dakota, and 600 and 700 miles, respectively, from the two Montana stations. The species has not been found in the intervening expanse of Rocky and Big Horn mountains. Are these few southern plants the remnants of its farthest southern push during glacial times and its wide northern distribution a reoccupation of territory lost during the Glacial Epoch?

2. *Salix petiolaris* J. E. Smith has much the same eastern distribution (fig. 2) as *S. serissima*. It ranges slightly farther south, occupying the northern third of Indiana and the two northernmost tiers of counties in Iowa as far west as the Mississippi-Missouri divide. The line then runs northwest to west-central Minnesota (Chippewa County), northeastern South Dakota (Day County), and adjacent North Dakota (Richland County), and thence passes through McLean, McHenry, and Bottineau counties, of central and north-central North Dakota, and on into Canada. The western border of its continuous distribution is somewhat farther to the south and west than that of *S. serissima*. It is a low clumpy shrub southward, becomes gradually larger northward, and is often a small tree in the Prairie Provinces, where it extends at least to Lake Athabaska.

Correlated with the somewhat greater western extension of its continuous distribution is its broader and deeper discontinuous penetration far to the south and west. Four separate areas are occupied by *S. petiolaris*, as verified by the following collections. 1.) The sandhills of northwestern Nebraska and adjacent South Dakota. Cherry County: Rowley Ranch near Kennedy, 1892, *Smith* and *Pound*, 1910–1914, *Bates;* Bear Creek and Dewey Lake, 1941, *Tolstead;* Oasis, 1912, *Pool* and *Nelson*. Bennett County (southwestern South Dakota adjacent to Cherry County, Nebraska): 1924, *Over*. Sheridan County: near Ellsworth, 1933, *Sandoz*. Brown County: Ainsworth, 1941, *Tolstead*. (The preceding three Nebraska counties are contiguous in north-central Nebraska westward; the following are farther south.) Thomas County: Purdum, 1901, *Baker*. Dawson County: 1943, *Kiener*, Arthur County: 1943, *Kiener*. 2.) The eastern face of the Black Hills of southwestern South Dakota in Custer, Pennington, Lawrence, and Meade counties: Jim Creek (T. 2 N., R. 5 E.) 1913, *Setzer;* Bear Butte Creek (T. 4 N., R. 4 E.), 1919, *Murdoch;* Castle Creek, 1924, *Over;* Castle Creek near Deerfield, 1928, *McIntosh;* near Merritt, 1924, *Over;* Squaw Creek, 12 miles above Game Lodge, 1926, *McIntosh;* Sylvan Lake, 1926, *McIntosh;* Custer, 1928, *McIntosh.* 3.) Estes Park, northern Colorado. Larimer County: Estes Park, elevation 7500 feet, 1933, 1934, *Ernest C. Smith* (seven collections). 4.) The Pikes Peak area in east-central Colorado. Teller County: east of Divide, 1935, *J. H. Christ.* El Paso County: Black Forest, 1935, *J. H. Christ.*

The sandhills area of Nebraska-South Dakota, and the Black Hills area of South Dakota, lie some 300 to 400 miles west-southwest of the margin of the continuous eastern distribution. The two mountain localities in Colorado are about 100 miles apart and 300 to 350 miles southwest of the Nebraska and South Dakota areas and therefore some 600 to 700 miles southwest of the margin of continuous distribution.

In the case of *Salix serissima,* there are four isolated and distant localities of discontinuous distribution, in three States. In the case of *S. petiolaris,* there are two relatively extensive areas and two isolated mountain localities of such distribution, also in three different States.

United States Department of Agriculture,
Washington, D. C.

SEED GERMINATION IN GILIA CAPITATA AND ITS RELATIVES

Verne Grant

The discovery that seeds of *Gilia capitata* Douglas (Polemoniaceae) collected from a recently burned hillside in the California Coast Ranges germinated twice as well as seeds from an unburned site in the same immediate area posed both the practical problem: how to obtain the highest percentage of germination from the seeds available for experimentation; and the theoretical problem: whether fire is a factor in the distribution of *Gilia capitata.* The observation, again, that the closely allied races, *G. chamissonis* Greene and *G. staminea* Greene, are confined in nature to pure sands on the California coast and in the San Joaquin Valley raised the question whether the distribution of these entities is related to the germination requirements of their seeds or the tolerances of their seedlings at establishment. Numerous germination tests, in which temperature, substrate, and other factors were varied, were then undertaken.

Like many other herbaceous elements in the California flora, *Gilia capitata* and its allies germinate with the first heavy rains of the fall. The spiracles of the seed coat imbibe water immediately upon being wetted and form a gelatinous sheath about the seed. Within a few days the embryo emerges and the pair of green cotyledons is soon raised above the ground. The seedlings with their first true leaves pass the winter from November until February or March in a semi-dormant condition; upon the first warm temperatures of spring they then resume growth.

METHODS

Seed collections in bulk and by families (individual seed parents) were made from the following strains of *Gilia capitata* and its close relatives in California: *G. capitata* from an open hillside swept by a surface fire during the year of seed collection, Mayacama Mountains, Napa County; *G. capitata* from the same hillside in a local oak grove not touched by the fire; *G. capitata* from Tomales Bay, Marin County; *G capitata* from Hatchet Mountain, Shasta County; *G. chamissonis* from sand dunes on Point Reyes Peninsula, Marin County; *G. chamissionis* from sand hills of San Francisco; *G. staminea* from sand hills near Antioch, Contra Costa County; *G. staminea* from Mather, Tuolumne County. (The foregoing entities are being treated by the author as subspecies of the polytypic species *Gilia capitata* in a monographic study which will shortly be in press.) In addition, seeds from experimental cultures and artificial hybridizations were obtained, as outlined in a subsequent paragraph.

Seed treatment was varied as follows:

1. Controls. Untreated seeds were planted in sand flats in the greenhouse.

2. Scarification. The seed coats were scratched between two pieces of sandpaper in a petri dish.

3. Stratification at constant temperatures. Flats containing the seeds were watered and stored immediately in a cold room for two, four, or six weeks at 2.5° C. or 5.0° C.

4. Stratification at alternating temperatures. The flats were stratified overnight at 5° C. and brought out into a warm room during the day. This process was continued for two, four, or six weeks.

5. Restratification. The stratified flats, after being removed to the greenhouse for germination, were subsequently returned to the cold room for a second treatment with cold temperatures, followed by a second period in the greenhouse (Quick, 1943).

6. Heating of seeds at 150° C. The seeds were placed in open petri dishes in an electric oven at 150° C. for 5 minutes, then planted in sand in the greenhouse and watered.

7. Heating of seeds at 750° C. The seeds were put in a small wire screen box which was then fastened to the end of a stick. A flash fire of excelsior was built in a fire place. At the height of the blaze the wire box containing the seeds was passed through the flames for three seconds.

8. Planting of whole capsules. The capsules of *G. staminea* and *G. chamissonis* are dehiscent and contain numerous, small seeds which are normally sprinkled out of the open ends with the swaying of the peduncles in the wind. The capsules of *G. capitata* in the Coast Ranges are by contrast indehiscent, 1–3-seeded, and tend to disarticulate and fall out of the calyx at maturity. In an effort to determine the possible adaptive significance of this latter combination of characters, undehisced capsules of *G. capitata* from the Mayacama Mountains were planted in sand in the greenhouse. The germination percentage was calculated on the basis of the estimated number of seeds present.

9. Stratification of whole capsules at 2.5° C.

10. Heating of whole capsules at 150° C.

11. Heating of whole capsules at 750° C.

12. Heating of whole capsules at 750° C. followed by immediate stratification at 2.5° C. in wet sand.

13. Washing the seeds in frequent changes of distilled water before sowing.

14. Sand in 6 inch pots in greenhouse. This was a control for the following three variations in type of substrate.

15. Autoclaved sand in greenhouse.

16. Adobe-clay in 6 inch pots in greenhouse.

17. Adobe-clay in the experimental field, Berkeley. Since the same parent soil was used here as in the greenhouse pots, the chief variable was soil temperature, which in spring of course was much lower outdoors.

The effect of genetic factors on seed germination was inferred in two ways:

The germination percentage of F_1 hybrid seeds was compared with the germination percentage for the parental entities. The seeds of both the species and the hybrids were harvested from plants growing under the same greenhouse conditions, and were planted and stratified side by side in the same flats.

Ten seeds from each of twenty-one randomly selected individual plants in the Mayacama colony of *G. capitata* were sown and their germination percentages were determined. This process was repeated for the seven strains under examination. The variance between strains was then compared with the variance between families.

Environmental Effects on Germination

The principal results are shown in Table 1, where the numbers heading the various columns correspond to the paragraph num-

Table 1. The Effects of Various Environmental Factors on Seed Germination in Gilia capitata and its Relatives. (The numbers heading the columns correspond to the paragraph numbers under "Methods.")

Treatment	1		3,4		8,9		6,10		7,11,12		14		16		17	
	Controls		2.5-5.0°C		Whole capsules		150°C		750°C		Sand, green-house		Clay, green-house		Clay, field	
Strain	% Germination	no. Seeds	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.
Mayacama Mts., unburned area	8	200	32	740	1	275	0	50	0	179						
Mayacama Mts., burned area	24	50	61	948			0	97			2	50	4	50	14	50
Tomales Bay	45	100	88	427												
Pt. Reyes	25	100	77	654							4	50	4	50	10	50
San Francisco			77	293												
Antioch			52	420							8	50	14	50	8	50
Mather	40	100	46	536												
Hatchet Mt.			31	366												

bers for methods of treatment; in certain columns the data for the two different treatments have been combined. The strain of *G. capitata* from the burned area in the Coast Ranges germinates much better than the strain away from the burn in both the controls and the stratified lots. Stratification increases the percentage and uniformity of germination in all strains. No significant difference was found between constant and alternating temperatures, between 2.5° C. and 5.0° C., or between two and six weeks stratification. After six weeks the seeds germinated in the cold room. *Gilia staminea* from four thousand feet elevation in the Sierra Nevada (Mather) appears not to require stratification any more than the lowland strains (cf. also Mirov, 1936).

When whole capsules of Coast Range *G. capitata* are sown, instead of thrashed seeds, the result is zero per cent germination without stratification, and one per cent (of the estimated number of seeds) germination with stratification.

The exposure of either naked seeds or whole capsules to 150° C., a temperature which some grass seeds withstand (Sampson, 1944), evidently injured the seeds for no germination at all was obtained. The temperatures of a flash fire are likewise deleterious to the seeds of *G. capitata* with or without the protective covering of the capsule.

As regards the effects of the substrate, *G. staminea* and *G. chamissonis,* both restricted to pure sands in nature, germinate and become established as well on clay-adobe as on sand.

Treatments which had no apparent effect were: use of autoclaved sand, washing the seeds with distilled water, scarification, and restratification. These experimental treatments have been omitted from Table 1. *Gilia capitata* differs in respect to the results of restratification from certain species of *Phacelia,* in which restratification is effective (Quick, 1947).

TABLE 2. FREQUENCY DISTRIBUTION OF GERMINATION PERCENTAGES BY FAMILIES IN SEVEN STRAINS OF GILIA CAPITATA AND ITS CLOSE RELATIVES. (ABOUT 21 FAMILIES PER STRAIN AND ABOUT TEN SEEDS PER FAMILY.)

Strain	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Mayacama Mts., burned area			2	1	1	4	4	1	6	1	1
Tomales Bay					1			1	3	6	11
Pt. Reyes			1		1		5	2	6	6	1
San Francisco			1	1		2	1	3	5	4	3
Antioch		3	2	2	2	3	5	2	1	1	1
Mather	5	1		2	2	1	3	1	4		
Hatchet Mt.	3	2	5	3	3	2	1	1	1	1	

GENOTYPIC EFFECTS ON GERMINATION

The germination of seeds from different seed parents (viz. families) of the same population is shown in Table 2. Undoubtedly there is great variation from family to family, as an examination of the germination percentages for the Mayacama strain of *G. capitata* will reveal. Analysis of the variance showed that there is significantly more variation between strains than within strains, but that the variation from family to family within one strain is much greater than would be expected if due to chance alone. The non-random variation in germination between families of one strain may be due to differential environmental influences on the seed parents, to genotypic differences between seed parents, or to both sets of factors. Similarly the differences in germination between strains may be due to differences in environment, genotype, or both.

Crosses between four of the strains would seem to indicate that germination behavior has a hereditary basis. The germination of the F_1 seeds is not intermediate with respect to that of the entities, but in most cases is better than either parental type (fig. 1). Whether this is to be taken as a manifestation of that debated quantity known as hybrid vigor depends on one's definition of hybrid vigor. The data suggest at least that germination percentage is in part under genotypic control.

Discussion

Gilia staminea and *G. chamissonis* are inhabitants of relatively loose sandy soils in nature. In cultivation the plants will flower and fruit in pure sand watered only with tap water; they thrive much better, however, if transplanted to richer soils. Germination tests show that the seeds germinate and the seedlings become established on adobe-clay in Berkeley under both field and greenhouse conditions. These facts taken together with the observation that *G. staminea* and *G. chamissonis* do not successfully withstand the competition of more aggressive species, either in

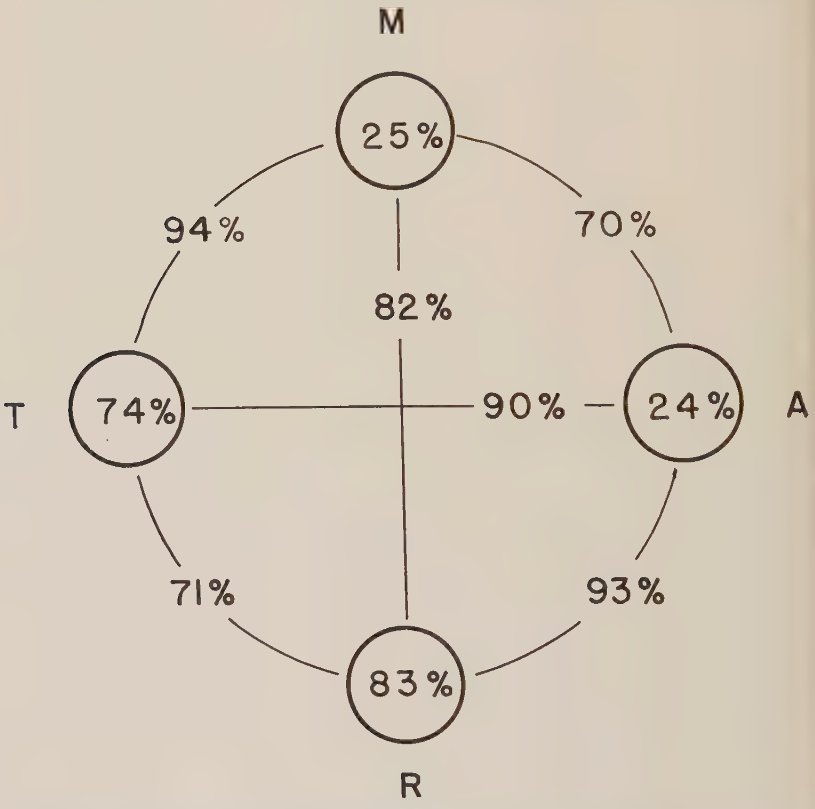

Fig. 1. Percentages of seed germination in four parental strains of *Gilia capitata* and its close relatives, and their F_1 hybrids. The parental strains are represented as circles. M, Mayacama Mountains; A, Antioch; R, Point Reyes Peninsula; T, Tomales Bay. In each case, percentages are based on 140 to 280 seeds.

nature or in the garden, suggest that the micro-distribution of *G. staminea* and *G. chamissonis* within their distributional areas may be the resultant of a tolerance for impoverished habitats and an intolerance of competition.

Gilia capitata occurs on sunny hillsides in the Coast Ranges. It is one of the commonest plants in clearings following a fire. Germination tests indicate that the seeds of *G. capitata* do not endure even moderately high temperatures. Certain other facts about this plant provide a clue as to the possible reasons for its abundance on burned areas; both field observations and garden tests show that *G. capitata* does not tolerate either deep shade or dense growth. With its annual life cycle and its low mineral requirements it is, like *G. staminea* and *G. chamissonis,* primarily a pioneering species on open habitats. Fire, by removing a more mature vegetation, returns the habitat to a stage suitable for colonization by *G. capitata.*

SUMMARY

1. There is marked variation between and within populations of *Gilia capitata* Dougl. and its allies as to percentage of seed germination. Some of this variation is genotypic; some of it is environmentally conditioned.

2. The seeds of both highland and lowland strains of *G. capitata* and its close relatives germinate relatively well when planted in moist sand without previous treatment. Stratification for two weeks at temperatures just above freezing improves germination. Restratification and scarification are ineffective. Brief exposure of the naked seeds or undehisced capsules of Coast Range *G. capitata* to temperatures of 150° C. or higher completely inhibits germination.

3. The micro-distribution of *G. capitata* and its allies is discussed in the light of the germination tests and some other observations. The confinement of *G. staminea* and *G. chamissonis* to sandy soils in nature, and the abundance of *G. capitata* in clearings following fires, may best be explained by regarding these plants as pioneers fitted for open habitats, but not tolerating the conditions of competition and shade in closed communities.

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LITERATURE CITED

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NOMENCLATORIAL CHANGES IN ARIZONA GRASSES

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The grasses of Arizona have long been a source of interest to both taxonomist and ecologist. Early collections and observations by Pringle, Lemmon, Toumey, Griffiths, Thornber, Blumer, and Goodding, and early range studies by national and territorial research units provide a substantial background for current investigations of our rich and diverse grass flora. Much of this accumulated information is being incorporated in a manual of Arizona grasses now being completed by the writer. To make the nomenclatorial changes deemed necessary for the manual more readily available the following new combinations and new names are herein proposed separately.

1. Panicum capillare L. var. **stramineum** (Hitchc. and Chase) comb. nov. *P. stramineum* Hitchc. and Chase, Contr. U. S. Nat. Herb. 15: 67. 1910.

2. Panicum capillare L. var. **hirticaule** (Presl) comb. nov. *P. hirticaule* Presl, Rel. Haenk. 1: 308. 1830.

3. Panicum capillare L. var. **pampinosum** (Hitchc. and Chase) comb. nov. *P. pampinosum* Hitchc. and Chase, Contr. U. S. Nat. Herb. 15: 66. 1910.

4. Sporobolus airoides (Torr.) Torr. var. **Wrightii** (Munro) comb. nov. *S. Wrightii* Munro ex Scribn., Bull. Torrey Bot. Club 9: 103. 1882.

5. **Elymus lanceolatus** (Scribn. and Smith) comb. nov. *Triticum repens* var. *dasystachum* Hook., Fl. Bor. Am. 2: 254. 1840. Not *Elymus dasystachys* Trin. ex Ledeb. Fl. Alt. 1: 120. 1829. *Agropyron dasytachum* Scribn., Bull. Torrey Bot. Club 10: 78. 1883. *Elymus subvillosus* (Hook.) Gould, Madroño 9: 127. 1947.

6. **Elymus Rydbergii** nom. nov. *Agropyron riparium* Scribn. and Smith, Bull. U. S. Div. Agrost. 4: 35. 1897. *Elymus riparius* Gould, Madroño 9: 127. 1947. Not *E. riparius* Wieg., Rhodora 20: 84. 1918.

7. Elymus pauciflorus (Schwein.) Gould subsp. **pseudorepens** (Scribn. and Smith) comb. nov. *Agropyron pseudorepens* Scribn. and Smith, U. S. Dept. of Agric., Div. Agrost. Bull. 4: 34. 1897. *A. tenerum* Vasey var. *pseudorepens* Jones, Contr. West. Bot. 14: 19. 1912.

8. Poa fendleriana (Steud.) Vasey var. **longiligula** (Scribn. and Williams) comb. nov. *Poa longiligula* Scribn. and Williams, U. S. Dept. Agric. Div. Agrost. Circ. 9: 3. 1899.

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DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See Madroño 9:257–258. 1948.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
LILIACEAE _Chlorogalum_ *_pomeridianum_ (Ker) Kunth.	$2n = 18_{II}$	M. S. Cave, Univ. Calif. Berkeley	_Cave 4901_ UC[1]	Contra Costa Co., Calif.
Odontostomum *_Hartwegii_ Torr.	$n = 10$	M. S. Cave, Univ. Calif. Berkeley	_Nobs 511_ UC	Placer Co., Calif.
RANUNCULACEAE _Actaea_ *_spicata_ L. var. _arguta_ Torr.	$n = 8$	R. L. Rodriguez, Univ. Calif. Berkeley	_Rattenbury 129_ UC	Contra Costa Co., Calif.
Kumlienia *_hystricula_ (Gray) Greene	$2n = 7_{II}$	Karl M. Jakob, Univ. Calif. Berkeley	_Rattenbury 202_ UC	Mariposa Co., Calif.
CALYCANTHACEAE _Calycanthus_ *_occidentalis_ H. & A.	$2n = 11_{II}$	M. S. Cave, Univ. Calif. Berkeley	_Cave 4903_ UC	Alameda Co., Calif.
CRUCIFERAE _Dentaria_ *_integrifolia_ Nutt. var. _californica_ Nutt.	$n = 22–28$	B. Crampton, Univ. Calif. Berkeley	_Rattenbury 128_ UC	Contra Costa Co., Calif.
ROSACEAE _Cercocarpus betuloides_ Nutt.	$2n = 9_{II}$	T. Morley, Univ. Calif. Berkeley	_Morley 99_ UC	Alameda Co., Calif.
POLEMONIACEAE _Gymnosteris_ *_nudicaulis_ (H.&A.) var. _pulchella_ (Greene) Brand	$n = 6$	C. McMillan, Univ. Calif. Berkeley	_Mason 13983_ UC	Washoe Co., Nevada
SCROPHULARIACEAE _Synthyris_ *_reniformis_ (Dougl.) Benth. subsp. _cordata_ Gray.	$n = 12$	C. McMillan Univ. Calif. Berkeley	_McMillan 1531_ UC	Marin Co., Calif.

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*Prepared slide available.

[1] Symbols used for herbaria are those listed by Lanjouw, Chronica Botanica 5: 142–150. 1939.

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REVIEW

Ethnobotany of Western Washington. By Erna Gunther. University of Washington Publications in Anthropology, Vol. 10, No. 1, pp. 1–62. October, 1945. University of Washington Press. $1.50.

This interesting study was originally intended as an investigation of the relationship of a people and its floral environment. Because of the presence of numerous small Indian tribes, belonging to five linguistic stocks but possessing a general homogeneity of culture and living in an area of relative botanical uniformity, western Washington appeared to be a particularly promising field. By showing specific plants to native informants it was possible to assemble data regarding their names and uses (as materials, medicine, or food) in the aboriginal cultures; additional data were compiled from published sources. It was found, however, that "the environment had changed too much, and the process of acculturation had gone too far" to allow full realization of the author's objectives. Nevertheless, interesting data were obtained concerning the uses of a large number of native plant species, including the following: *Polypodium vulgare, Polystichum munitum, Dryopteris dilatata, Athyrium Filix-foemina, Adiantum pedatum* var. *aleuticum, Struthiopteris spicant, Equisetum* spp., *Taxus brevifolia, Pinus monticola, Picea sitchensis, Tsuga heterophylla, Pseudotsuga taxifolia, Thuja plicata, Typha latifolia, Lysichitum americanum, Xerophyllum tenax, Zigadenus venenosus, Veratrum Eschscholtzii, Allium cernuum, Camassia Quamash, Lilium columbianum, Maianthemum dilatatum, Trillium ovatum, Populus trichocarpa, Salix* spp., *Corylus californica, Alnus oregana, Quercus Garryana, Urtica Lyallii, Claytonia sibirica, Aquilegia formosa, Actaea arguta, Berberis* (*Mahonia*) spp., *Dicentra formosa, Philadelphus Gordonianus, Ribes* spp., *Physocarpus capitatus, Holodiscus discolor, Spiraea* spp., *Aruncus sylvester, Rosa* spp., *Rubus* spp., *Fragaria* spp., *Geum macrophyllum, Prunus emarginata, Osmaronia cerasiformis, Amelanchier florida, Pyrus diversifolia, Vicia* spp., *Oxalis oregana, Acer* spp., *Rhamnus Purshiana, Epilobium angustifolium, Oplopanax horridum, Heracleum lanatum, Oenanthe sarmentosa, Cornus* spp., *Gaultheria Shallon, Arctostaphylos Uva-ursi, Vaccinium* spp., *Prunella vulgaris* var. *lanceolata, Stachys ciliata, Galium triflorum, Sambucus* spp., *Symphoricarpos albus, Lonicera* spp., *Achillea Millefolium, Petasites speciosus,* and others. The plants were determined by Dr. G. N. Jones and Mrs. M. R. Flahaut, and a partial set of verifying specimens is deposited in the herbarium of the Washington State Museum in Seattle.—L. Constance, Department of Botany, University of California, Berkeley.